XIV. *An Account of some Experiments on the Edibility of certain* Lepidopterous *Larvae.* By H. Eltringham, M.A., F.Z.S.

[Read October 6th, 1909.]

For a considerable period, following on the first enunciation of the theories of Batesian and Müllerian mimicry and common warning colours, the criticism that these theories were based on small practical evidence was to some extent justified. Such criticism, however, did not in any way invalidate the theories in question. It had also the highly salutary effect of acting as a stimulus, not only to the upholders but also to the opponents of these theories, to carry out practical experiments with a view to obtaining actual evidence bearing on some of the points involved.

It is a matter of common knowledge amongst those who have studied these subjects, that the experiments which have been recorded all tend to support the now well-known theories of mimicry which had their origin in the celebrated arguments published nearly fifty years ago by Mr. H. W. Bates. Amongst the many points to be elucidated, one of the most important was the proof of the comparative inedibility of many insects. For much valuable evidence on this head we are indebted to the experiments of Mr. Jenner Weir, Mr. A. G. Butler, Prof. Weismann, Mr. F. Finn, and especially to those of Prof. Poulton and Mr. G. A. K. Marshall, and it can no longer be said with justice that the hypothesis of the comparative distastefulness of most warningly coloured insects rests on insufficient evidence.

Arising out of the foregoing experiments, one of the results obtained by Prof. Poulton * was as interesting as it was unexpected. Whilst in accordance with anticipation, warningly coloured larvae were found to be distasteful, and cryptic larvae edible, one instance was discovered in which a larva (that of *Mania typica*), though exceedingly

* Proc. Zool. Soc. 1887, Experimental Proof of the Value of Colour and Markings in Insects in Reference to their Vertebrate Enemies.

well protected by its colour and habits, proved to be distasteful to the lizards which were being used for the purpose of the experiments. The importance of this result is fully discussed by the author,* who points out that we have here an instance in which the distasteful qualities are present as an accidental and useless character, but providing an excellent example of how the distasteful properties of many forms may have existed prior to the development of warning colours, conditions being thus favourable to the development of the latter in the event of any change being brought about in the larval habits.

It was in the hope of perhaps discovering another case of a similar character, that I decided to carry out some experiments with the only insectivorous creatures which were available, viz. lizards, and with such larvae as I was able to obtain.

Two green lizards (probably *Lacerta viridis*) were installed in a fairly large vivarium, and their number was subsequently increased by the addition of three more of the same small variety, and two fine examples of the larger Channel Islands form. There were also two orange and black salamanders, but these proved to have such poor appetites that they provided very little information.

The general results of feeding the lizards with various insects confirmed those already obtained by other observers, though there were some unimportant exceptions. The larva of *Picris brassicae* is recorded by Prof. Weismann as having been refused by his lizards. I found that on some occasions it was eaten, though with considerable hesitation and usually when the animal was hungry. One of the salamanders refused it after examining it carefully for some time. Earthworms were eaten with avidity, and "blue-bottles" (*Calliphora vomitoria*) were always taken with evident relish. The larva of *Spilosoma lubricipeda* was generally refused, though the lizards took considerable interest in it. One lizard followed the larva round the cage for some time, feeling it with its tongue, but the hairs always put it off, and it was finally abandoned. A young larva not so hairy was eaten on one occasion after some trouble with the hairs, a fact which seems to suggest that the protection is mechanical and not due to actual distastefulness. A "devil's coach-horse" (*Ocypus olens*) was eaten, though the operation took a considerable time,

* *L. c.*, p. 241, *et seq.*

and once the beetle appeared to nip the lizard with its mandibles, as it dropped it suddenly and went through surprising contortions.

The imago of *P. rapae* was eaten with apparent relish, as also that of *Plusia gamma*. Green and greenish-brown larvae of cryptic habits were eaten, as also were the extremely cryptic geometrid larvae of *Amphidasys betularia* and *Selenia lunaria*. A bee was attacked and dropped, though the salamanders ate bees with impunity. The most interesting results were obtained with the larvae of *Boarmia rhomboidaria*. This larva was found in large numbers feeding on ivy. Probably few British larvae have attained to a more perfect development of cryptic form, colour and habit than this species. It resembles so perfectly the twigs of the ivy that it is frequently only possible to detect it by the sense of touch. If thrown down it will often lie perfectly straight and motionless, when it is practically indistinguishable from a small piece of stick. According to the general rule it would be expected that this larva when detected would prove to be as palatable as *betularia*, *lunaria*, and other similar forms. My experiments, however, proved that quite the opposite is the case. I was interested to discover whether this unpalatability could be traced to any definite secretion, such as potassium hydroxide. A crushed larva gave a slight alkaline reaction with litmus paper, so I boiled a considerable number of the larvae and tested the filtered solution. The alkalinity was, however, so slight that it seemed unnecessary to pursue the examination in this direction, and it appeared probable that the food-plant might be directly responsible for the chemical reaction. This again proved not to be the case, as the crushed shoots of ivy were found to be slightly acid.

As the larva in question will eat other plants than ivy it occurred to me to try the effect of a change of food-plant on its edible properties. I found that after being fed on apple for from two to three days and onwards, the distasteful properties disappeared and the apple-fed larvae were eaten without any hesitation.

I herewith append notes from my journal made at the time of each experiment, in order that those interested may judge of the results for themselves.

August 29.—A salamander ate an earthworm, then a bee (without apparently being stung), and then another

worm. It then very carefully inspected a larva of *P. brassicae*, started backwards slightly, and finally refused to look at it.

One lizard ate a small worm, then part of a larger one; it then examined a larva of *brassicae* and seized it, holding it in its mouth by a very small grip of the skin for about three minutes, then it bit it harder and put it out. Then it picked it up very doubtfully and swallowed it very slowly. The other lizard, which had had nothing for at least two days, seized the same kind of larva and swallowed it, apparently without compunction; it then rubbed its nose against the glass of the cage for some time, and once appeared to writhe on the floor. Later on it was offered another of the same larvae, but it would have nothing to do with it. It then turned round and bit the other lizard twice, though the object of this manœuvre was not apparent.

August 30.—One of the lizards tried to eat a larva of *rhomboidaria*, but left it after two attempts.

August 31.—A lizard after some hesitation appeared to swallow one of these larvae, but a moment later vomited it up again, ran violently round the cage, and then drank some water. A few hours later it bit another, but put it out and rubbed its nose on the pebbles.

September 1.—The other lizard behaved in exactly the same way this morning. The first lizard was given a larva of *Spilosoma lubricipeda*. It followed it all round the cage feeling it with its tongue, but though it evidently wanted to try it the hairs put it off, and it finally abandoned it. After this neither lizard would eat anything.

September 2.—One lizard examined a larva of *S. lubricipeda*, but the hairs put it off. Then each lizard ate a worm, and one subsequently ate a larva of *P. brassicae* rather slowly, putting it out once but finally swallowing it. Later in the day one lizard attacked a "devil's coach-horse" (*Ocypus olens*). It took about half-an-hour to eat it, continually dropping it and picking it up again. Once it dropped it suddenly and went through the most violent contortions, rubbing its head sideways and half burying itself under the gravel. Whatever the cause of this may have been, it again picked up the beetle and began to swallow it; apparently it had the greatest difficulty in doing so, as it shook it out of its mouth several times. Ultimately, however, it got it down.

September 3.—One lizard ate three blue-bottles and a *P. rapae.* The other one ate a green caterpillar (probably *Hadena oleracea*). Neither would touch a larva of *rhomboidaria.* Later on the first lizard ate another *P. rapae,* and the second ate two brownish-green larvae taken off chrysanthemum plants.

September 5.—Lizards had nothing to eat yesterday. This morning one of them ate a blue-bottle, and I then offered it a larva of *rhomboidaria.* It seized it by the tail and held it in its mouth for a short time, then worried it furiously. As soon as it got a little more into its mouth it dropped it and began rubbing its mouth violently on the floor of the cage. Afterwards it would not look at it again. The larva was still alive and the other lizard came and looked at it, but either smelt it or recognized its appearance, as it would not bite it. The first lizard immediately afterwards ate a "blue-bottle," and about two hours later a small earthworm. The manner in which it swallowed these was very different to that in which it treated the caterpillar. There was no hesitation, and the worm was gulped down very rapidly.

(Note.—These lizards ate larvae of *P. brassicae* but slowly, and as though not greatly appreciating them.)

Later in the day one lizard ate four "blue-bottles" and a *P. rapae.* The salamander ate three bees. The lizard snapped up a bee but dropped it again suddenly, as though stung, and would not look at another.

September 7.—Lizard ate two "blue-bottles," a brownish-green larva from the chrysanthemums, and a "gamma" moth.

The other lizard ate a larva of *rhomboidaria* which had been fed on apple for two days. While it was eating it the other lizard chased it round and round the cage. A second apple-fed larva was refused by both lizards. Later on one lizard ate a worm but tasted and refused a wood-louse.

September 8.—First lizard would not look at an apple-fed *rhomboidaria* larva, but the other one ate it, rather slowly at first. An ivy-fed one was then offered, but neither lizard would touch it. The first lizard then ate two "blue-bottles."

September 9.—Five more lizards arrived.

One of the original pair ate an ivy-fed caterpillar with some hesitation, afterwards drinking water. One of the

new lizards, presumably hungry, was given an ivy-fed larva of *rhomboidaria*, it bit it and then dropped it, going through violent contortions and rubbing its nose on the pebbles. A little while later it was given a larva which had been fed on apple for four days. It ate it without any hesitation. It was then offered the ivy-fed larva which it had before refused, and after some hesitation it swallowed it, though evidently without any keenness. Another of the new lizards was then offered an ivy-fed larva. It bit it and dropped it suddenly, rubbing its nose on the pebbles. It then took another bite and put it out again, opening its jaws wide and then rubbing its nose on the floor. After a while it was induced to try an apple-fed example, which it swallowed rapidly after a short hesitation. The ivy-fed larva previously refused was then again offered, but it would not touch it.

One of the original lizards ate a larva of *betularia* and one of *lunaria*, but smelt and refused an ivy-fed *rhomboidaria*.

September 10.—A large lizard ate an ivy-fed larva with considerable hesitation, putting it out four times. This lizard had had nothing to eat for some days. After this it ate another ivy-fed larva with rather less hesitation. A third was seized by it and another lizard. They fought over it furiously, and the caterpillar was pulled in two and each swallowed its own piece. The competition apparently had something to do with the result, as immediately after the second lizard bit another larva and dropped it, rubbing its nose violently. A third lizard came up and examined the larva, when the other seized it again but dropped it like a hot coal. Another lizard twice examined and refused one of these larvae.

September 11.—A lizard ate rapidly and without hesitation two larvae of *betularia* and a "green-bottle." An ivy-fed *rhomboidaria* was then offered, but it examined it carefully and refused to touch it.

September 12.—An ivy-fed larva was offered to one of the lizards. It seized it at once and nearly managed to swallow it, but suddenly ejected it and rubbed its nose violently on the pebbles. After this it would not even eat a "blue-bottle," and an apple-fed *rhomboidaria* was disregarded. One of the large lizards was given a *rhomboidaria* larva which had been fed on apple for about a week. It seized it and ate it at once. It was then

given another taken from the ivy. It seized it at once and gave it two bites, dropped it and rubbed its nose on the pebbles. The original two lizards were offered ivy-fed caterpillars, but after inspection they would not touch them. They appear to have learnt that they are not good to eat. Another lizard seized an ivy-fed larva, but after two bites dropped it and rubbed its nose. It subsequently ate a "blue-bottle." Another lizard ate a young larva of *lubricipeda*, though the hairs bothered it a good deal at first, the lizard being apparently either pricked or tickled. An older and more hairy larva was examined, but refused on account of the hairs. Greenish larvae (probably *Hadena oleracea*) were eaten without hesitation.

September 13.—During a short sunny interval one of the large lizards came out and tasted an ivy-fed larva, but dropped it after two bites and rubbed its nose. It would not eat anything else after this.

Soon after the last-named date I was called abroad for a time, and was therefore unable to continue the experiments. Nevertheless it appears to me that extremely interesting conclusions may reasonably be drawn therefrom. It should be remembered that the mere bald statement that a lizard did or did not eat a certain insect scarcely supplies that conviction which the actual carrying out of the experiments conveys. The behaviour of the reptiles when dealing with their food gives a vivid impression of the degree of relish with which each particular morsel is consumed, and I am quite convinced by carefully watching the lizards that ivy-fed larvae of *Boarmia rhomboidaria* are extremely distasteful, and I am equally persuaded that when fed for a time on apple those distasteful qualities are removed. Ivy-fed larvae were tasted and refused with disgust seventeen times, and eaten five times. Even on the mere figures the evidence of distastefulness is ample, but in the cases where the larva was eaten, it was consumed with hesitation and evident lack of relish, whilst once it was eaten under stress of competition, the influence of which is hinted at by the example of the lizard which had tasted and refused the larva making a second attempt to eat it when threatened with interference by another of the reptiles. In strong contrast to this behaviour is the fact that apple-fed larvae were eaten in every case in which they were tasted, such hesitation as was shown being due to association with the

appearance of the previously discarded ivy-fed example whilst an apple-fed specimen was in no case rejected and again seized, but always swallowed uninterruptedly and without any of the characteristic nose-rubbing and other contortions which accompanied the dealings with those fed on ivy. From these facts it seems quite reasonable to conclude that when feeding on apple this highly cryptic larva remains as edible as are most other insects which are well protected by their colour, shape, and habits. The caterpillar is even better protected on ivy owing to the density of the foliage and the irregularity of the twigs, and yet when on that plant it becomes extremely distasteful, and furnishes an exactly similar case to that of *Mania typica*, discovered and described by Prof. Poulton. We thus have further evidence that the distasteful qualities of larvae may have arisen in similar accidental ways, and the difficulty of those "first steps" in evolutionary changes are still further decreased. We can see how a cryptic larva which occurs on a certain food-plant might be sought out and discovered by its enemies, and if the latter were sufficiently numerous and persistent, the insect might be exterminated. If, however, the larva can adapt itself to a change of food, it may gain some respite until again discovered. This may bring about a great change in the creature's method of defence. Its new food-plant endows it with inedible properties, and thus the insect has a further opportunity of developing a new mode of protection along different lines. To extend such reasoning, it seems not impossible that a purely Batesian mimic might become a Müllerian mimic by the same method. Batesian mimics are much associated with their models during life, and the instinct which guides a butterfly to lay its eggs on the right food-plant is not invariably infallible. Thus ova of an inedible species deposited on a new food-plant might conceivably give rise to larvae which survived and produced distasteful butterflies; and whilst the fact of such an occurrence may remain unproved, its evident possibility should serve to remind us once more of the complicated conditions under which butterflies in common with other creatures maintain their existence in the struggle for life.

(Note.—I am indebted to my friend, Commander J. J. Walker, for kindly identifying the Geometrid larvae above described.)